SOIL ANIMALS AND SOIL FABRIC PRODUCTION: FACTS AND PERCEPTIONS

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Quaestiones Entomologicae
21: 587-594 1985

ABSTRACT

Soil is composed of microenvironments resulting largely from distinct biological inputs or activities. These microenvironments in turn foster development of microcommunities which, in composite, determine patterns of soil micromorphology. Biological processes contribute to the local dynamics of microcommunities, bring about changes in soil structure, and are major features of soil function. Various spheres of influence, based upon soil microcommunities organize biologically mediated interactions between soil structure and soil function.

RÉSUMÉ

Le sol se compose de microenvironnements qui résultent principalement d'énergies ou d'activités biologiques distinctes. En retour, ces microenvironnements promouvoient le développement de microcommunautés qui, dans leur ensemble, déterminent les différents aspects de la micromorphologie du sol. Les processus biologiques contribuent à la dynamique locale des microcommunautés, modifient la structure du sol, et sont parmi les plus importants aspects de la fonction du sol. Diverses sphères d'influence, qui originent des microcommunautés terricoles, organisent, par l'entremise d'agents biologiques, les actions réciproques entre la structure et la fonction du sol.

INTRODUCTION

The contribution of soil animals to production and maintenance of soil fabrics is a vital part of soil function., Being a complex system, soil must be investigated in a holistic way so as to include the influence of soil animals.

Soil litter is the major source of organic input at the interfaces with the abiotic mineral soil. Soil litter is composed of a variety of plant parts including various species of leaves, seeds and fruits, other dead plant tissues - woody and herbaceous, fungal fruiting bodies, rhizomorphs and other microbial tissues. Animal contributions to litter are of all types and sizes: fecal masses and pellets, nesting materials and various forms of shed skins, egg shells and carcasses. Litter may appear as a zone of very high entropy, but when viewed in a more microscopic sense, order abounds, and within a very short time interbiotic and biotic - abiotic organization reaches high levels of fidelity. Cybernetic information is stored and patterns become more predictable soon after litterfall. Each litter component, being of different taxonomic origin or morphological form, provides a unique mass of highly organized elements, compounds and energy sources, and is a potential microhabitat. Each type of microhabitat, dependent upon its origin or form, further supports a predictable microcommunity of associated soil organisms predominantly decomposer microorganisms and invertebrates - the decomposer food web (Dindal, 1971;

1980). Decomposer microcommunities are structurally and functionally unique (Dindal, 1971; 1978a,b). When we think of the array of litter microcommunities as intricately related to abiotic soil components, a microecosystem paradigm emerges. Furthermore, the micromorphology of the soil fabric is an expression of microcommunity structure and function. Biological mediation, therefore, is vital at interfaces within the soil, and entropy of the soil ecosystem is continually lessened by these biotic activities. The microecosystem/microcommunity concept provides an obvious link connecting the abiotic, vegetative and vertebrate animal characteristics of any macroecosystem; thus a holistic approach to the understanding of soil fabric production is imperative.

AUTUMN OF LIFE

Litter Fall

An obvious component of soil litter is the mass of deciduous leaves shed annually within a temperate forest. In a northern hardwood forest in central New York (dominated by sugar maple, *Acer saccharum* Marsh, and ash, *Fraxinus* spp.) all of the leaf canopy was shed in 167 days (October 3, 1979 to January 17, 1980) with 86% of the leaves falling during the first 24 days. Surface area of fallen sugar maple leaves during this autumn was $3.6 m^2/m^2$ of soil surface (Dindal and Dindal, unpubl.). Also, we found the majority of the leaf litter was incorporated on site by the following April (Tardiff and Dindal, 1980); thus the potential physical and chemical properties of the previous leaf litter fall are accessible within soil by the following growing season. Such a rapid rate of input of organic compounds and fiber via leaf material is of considerable ecological significance related to soil structure and micromorphology.

Earthworms, *Lumbricus terrestris* L. (Hamilton, 1983) and isopods, *Oniscus asellus* L. were the dominant biotic mediators of incorporation of of leaf litter on the New York site. The remainder of the maple leaves, not consumed by earthworms, were skeletonized by the isopods, with the removal of 91% of the leaf (mostly mesophyll and palisade tissues) leaving the 9% fibrovascular bundle leaf structure intact. The obvious increase in surface area resulting from skeletonization is phenomenal; isopods reprocess leaf tissue into numerous fecal pellets each with an average surface area of 3.3 mm^2. Each pellet is a rectangular solid averaging 1.1 mm long with a 0.6 mm square end. In addition to the incorporation of these pellets into the soil, *Oniscus* also produces a network of 0.33 m^2/m^2 of fibrovascular bundle "lace" destined for soil microsites. This network provides potentially active sites with capacity for cation exchange and a cellulose/lignin matrix onto which soil minerals may be further physically and chemically bound.

Carrion Deposition

Carrion, invertebrate exuviae and carcasses of vertebrates comprise important components of soil litter even though they are less obvious or deliberately ignored. Carrion falling to the soil surface deposit various elements, biochemical compounds and energy sources that support decomposer food webs. Heterotrophic microcommunities quickly colonize, use and distribute the structural ingredients of highly proteinaceous vertebrate carcasses. Nitrogenous and sulphur laden compounds seep into the adjacent soil. Molecules that are naturally recalcitrant, like chitin which contains nitrogen radicals, scleroproteins with both nitrogen and sulphur moeities, calcium and magnesium carbonate-protein complexes and even organosiliceous compounds, can originate from decay of invertebrate and vertebrate carcasses. They are buried, directly or indirectly, providing unique slow release compounds as well as extraordinary organic matter substrates on which and from which soil fabric is produced.

Fecal Rain

Animal defecation constantly subjects the earth's surface to a "rain" of feces. These nutrient/energy-rich additions to soil sediments are extremely subtle, even more so than the fall of carrion. Perhaps the holistic effects of this omnipresent phenomenon would never be totally appreciated unless *all* organisms evacuated at exactly the same moment! Because defecation is a natural packaging, recycling process by which biochemical compounds and energy sources are pelletized, it is very important to soil formation and to dynamics of decomposer food webs. Fecal structure, chemical composition, pellet size, and rate of deposition are species specific. These characteristics represent a wide array of variables that are interjected into substrates of all ecosystems. Fecal pellets or dung balls are, therefore, energy/nutrient dissemules that are formed, transported and distributed onto the earth's soils by all kinds of animals.

SPECIFIC BIOTIC PROCESSES AT ORGANIC/INORGANIC INTERFACES

Total functions of decomposer microcommunities in association with unique microhabitats are responsible for processes such as soil fabric production, translocation, and transformation which ultimately lead to fabric reorganization and "soil ripening" as per Bal (1982). These are part of the biological activities referred to by Kubiena (1948) as the "principal driving forces of any soil forming processes." Several biologically mediated processes warrant more specific comment.

Slime and Gum Production

Mucopolysaccharides and other carbohydrate complexes are produced by many soil decomposer organisms within their soil/litter realm. Slimes and gums are exuded as metabolic byproducts, lubricants for mobility, forms of chemical and physical defense, modes of substrate attachment, and mechanisms for food-getting and pheromonal dispersal agents. In addition to their adaptive roles, these compounds may directly or indirectly cause or aid in formation of soil aggregates causing organic and abiotic materials to adhere forming erosion-stable units. In turn, this gives specific character to both the micro- and macro-structure of soil, *i.e.*, increasing organic matter incorporation, water holding capacity, porosity and ion exchange capacities. Also, the metabolism of the soil ecosystem is enhanced by the subtle monomolecular layers of slime that are potentially important microsubstrates for soil microbial colonization and population maintenance.

Coprophagy and Geophagy

Eating soil or mineral materials - *geophagy* (Jones and Hanson, 1985; Kramar, 1973), and consuming another individual's feces (either interspecifically or intraspecifically) - *coprophagy* (Hassall and Rushton, 1985; Simmons, 1983; Anderson, 1978; Kenagy and Hoyt, 1980), is not uncommon in the natural world. With future research, many more examples involving soil animals are likely to be documented. In the observed examples of coprophagy, a diversity of organic compounds, already subjected to an initial digestion are further subjected successively to the digestive processes and gut symbionts of new consumers. Inorganic and organic substances are forced together very closely within a gastrointestinal microhabitat and eventually incorporated into the soil matrix. Large fecal masses or pellets are altered chemically; they are reduced to smaller and smaller units, increasing in surface area and thus having particular impacts on the soil micromorphological structure and function.

Insertion of Organic Matter

Both invertebrates and vertebrates exhibit habits that cause many forms of organic matter to be inserted into soil thus modifying the soil fabric. Mammal burrows filled with organic material within soil profiles were recognized as Krotovinas by early agronomists. Birds which nest in ground burrows, such as the burrowing owl (*Speotyto cunicularia*), bank and cliff swallows (*Riparia r. riparia* and *Petrochelidon pyrrhonota*) and the belted kingfisher (*Megaceryle a. alycon*) all deposit and interject various organic compounds during production of their annual broods. Along sea coasts and above intertidal lines, crabs regularly bury carcasses and other organic debris. Dung beetles (Stevenson, 1983; Brussard, 1985), some spiders like *Geolycosa* (Shelford, 1913), ants, and enchytraeid and lumbricid worms constantly bury or intertwine organic matter with soil particles. Dipteran maggots migrate from their decayed food source, burrow and then pupate within the surrounding soil; most edaphic pupae die and decay in this buried state (Dillon, 1984; Hall, 1947).

Although each interposition of organic substance may be relatively microscopic when viewed from the macroecosystem level, the constancy of pattern, the regularity and ultimate sum of biotic input via these subtle and mundane processes greatly influences soil micromorphology and structure. Such active processes led Jenny (1980) to classify soil invertebrates functionally as "mechanical blenders" of soil. The insertion-upwelling activities are perhaps analogous to the action of the sewing machine where organic compounds are threaded into soil fabric following a specific spatial and temporal pattern; each stitch, no matter how minor, has its functional and structural role.

Upwelling of Inorganic Matter

Certain soil animals are responsible for mining and deposition of large quantities of mineral materials on soil surfaces. Burrowing rodents unearth and build surface mounds that have the heterogenous physical characteristics and textures of deeper soils. Upwelling not only influences the below-ground soil fabric but also noticeably shapes the surface landscape, whether caused by mound-building ants (Werner, 1984) or by fossorial rodents (Cox, 1984). Less noticeable, but of equal importance, are the excavations of mineral soil by non-mound building ants and earthworms. In a central New York old field, 78% of the mineral soil particles excavated by the ant, *Lasuis niger neoniger* Emery, are within the 180–425 μm size range (Dindal, pers. obs.). Possible species specificity of size selection of soil particles and movement by ants is probably an important factor in soil formation. We observed species specificity of soil aggregate (fecal casting) size formation relative to several dominant earthworm species (Dindal, Theoret and Moreau, 1978); also *Lumbricus terrestris* populations are highly correlated with presence of 4.0 mm water-stable soil aggregates (Hamilton, 1983). From these studies specific size relationships of soil aggregates to their biotic source are suggested (Table 1).

Gradual Comminution

Constituents of ingested plants and animals are radically transformed into complex forms and new compounds as they pass through the guts of large and small grazers and carnivores. These materials are microbially primed and again low entropy is facilitated (this time by

Table 1: PROPOSED SIZE RELATIONSHIPS OF EROSION-STABLE SOIL AGGREGATES TO EARTHWORM SPECIES AND THEIR SYMBIONTS.

SOIL AGGREGATE SIZE (mm)	SOIL BIOTIC SOURCE OF FORMATION
> 6.4	Symbiotic complex of earthworms, roots and microorganisms
4.0	*Lumbricus terrestris* L.
2.0	*Aporrectodea tuberculata* (Eisen)
1.0	*Octolasion tyrtaeum* (Savigny)
0.5	*Lumbricus rubellus* Hoffmeister
0.5	*Dendrobaena octaedra* (Savigny)
0.25	*Dendrodrilus rubidus* (Savigny)
0.15	Microorganisms

symbiotic relationships) as the food bolus is gradually transposed into feces.

Expelled remnants of ingesta that are packaged in dung pellets provide two surface area configurations different from the original form of the food. The initial size and surface area of the fecal pellet are functions of the rectal and cloacal organs and the anal cross-section. Species specific pellet size determines potential interspecific coprophagic efficiency and provides a unique microbial substrate within the soil microecosystem. As the pellet breaks down, a second potential surface area increases dramatically as dung constituents are exposed. These materials are the function of mastication, peristalsis and digestive activities and represent the maximum size reduction of food eaten by a given consumer. These secondary particles, which are finely divided, blend with the surrounding mineral particles and thus reflect the specificity of the animal species on soil formation.

For example, the surface area of the fragments of herbaceous fabric comprising fecal pellets of the cottontail rabbit, *Sylvilagus floridanus*, in central New York is 10 times greater than the surface of the individual entire ovoid pellet (Figure 1). Such a modification in the vegetation of the secondary fecal fragments deposited on or in the soil greatly increases the potential for organic/inorganic interfaces. Microbial and decomposer invertebrate activity, which is vitally important in the genesis of soil micromorphology, is stimulated.

SUMMARY

Understanding soil fabric production demands a holistic, cybernetic approach; this includes a multivariate consideration of all physical, chemical and biological intricacies of the soil, both macroscopic and microscopic, within ecological spheres of influence. The rhizosphere was one of the first of these ecological spheres of influence to be recognized, illustrating the microhabitat/microcommunity dynamics related to plant root systems. Phyllospheres have been conceptualized to study aerial microhabitats and microcommunities on surfaces of living leaves (Preece and Dickinson, 1971). We described the vermisphere (Hamilton and Dindal, 1983), another ecological sphere of influence within soil, which shows delicate biotic/abiotic

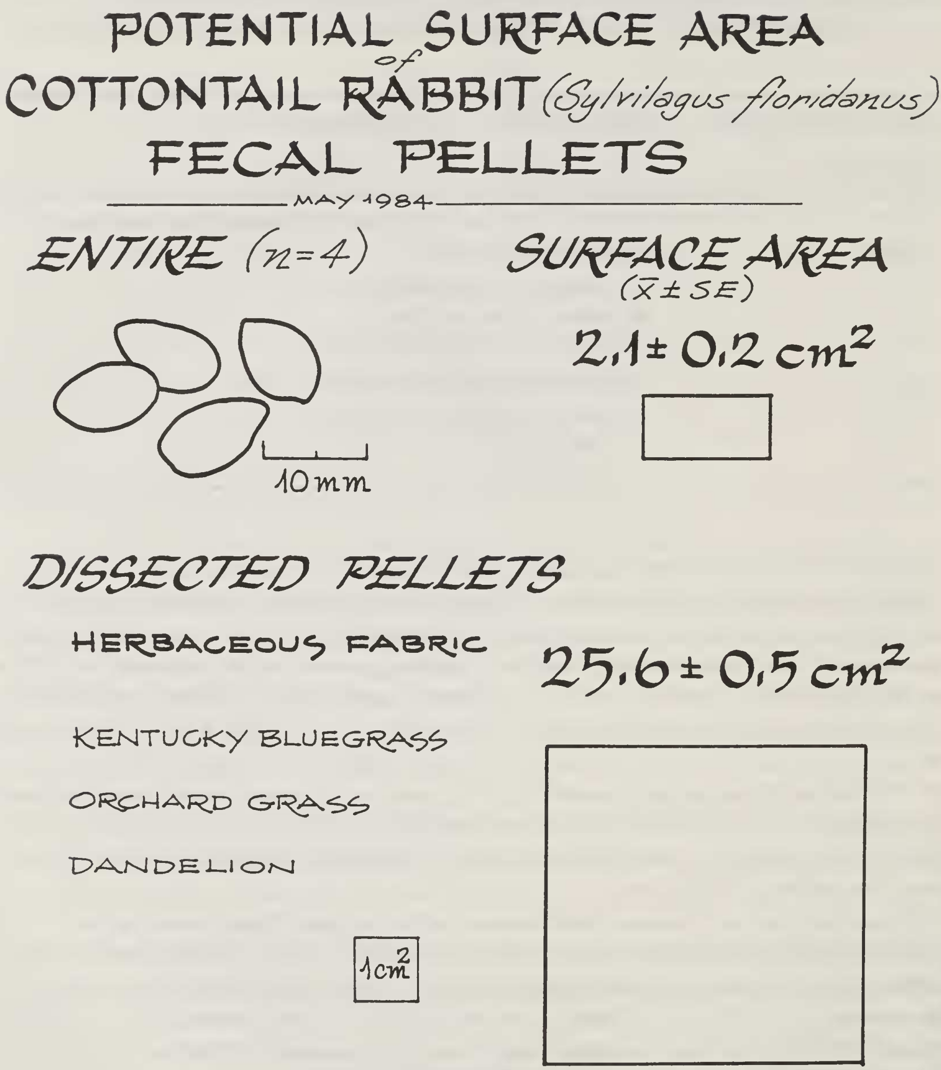
POTENTIAL SURFACE AREA of COTTONTAIL RABBIT (Sylvilagus floridanus) FECAL PELLETS
MAY 1984
ENTIRE (n=4)
10 mm
SURFACE AREA ($\bar{x}$ ± SE)
2,1 ± 0,2 cm²
DISSECTED PELLETS
HERBACEOUS FABRIC
KENTUCKY BLUEGRASS
ORCHARD GRASS
DANDELION
1cm²
25,6 ± 0,5 cm²

Figure 1.

interactions associated with earthworm burrows. Based upon unique soil microcommunities and related microhabitats emphasized in this paper, I propose the following additional microecosystem concepts to aid in research, communication and understanding of animal involvement in soil fabric production:

1. Edaphophyllosphere (=edaphic phyllosphere) - sphere of influence of the fallen leaf and vegetative litter as a soil microhabitat,
2. Coprosphere - sphere of influence of vertebrate and invertebrate fecal material as a soil microhabitat,
3. Necrosphere - sphere of influence of vertebrate and invertebrate carcasses as soil microhabitats,
4. Nidusphere - sphere of influence of vertebrate and invertebrate nests, nest sites and burrows as soil microhabitats.

The active result of the structure and function of the specific microcommunities inhabiting each of these microecosystems governs the immediate soil fabric formation and plays an ultimate influential role in the characteristic genesis and maintenance of any given soil.

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